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Female Preference for Male Coloration and Size in the Guppy, Poecilia Reticulata.

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Female preference for male coloration and size in the guppy, *Poecilia reticulata*

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ABSTRACT

In order to assess the female guppy's choice of male companion, females were allowed to choose among three differently colored or two sizes of males. The females were in complete control of the choice situation since the males were prevented from initiating any contact with them. The females chose males on a basis of color but not size, demonstrating that females chose some male guppies over others because of their physical characteristics.

Although the guppy, Poecilia reticulata, has been used as an experimental animal for many years, and its mating and courtship behaviors are well known, few studies have been concerned with the female's role in guppy courtship. This is surprising in the light of the concept of sexual selection, because presumably the female makes the final choice in courtship decisions (Trivers 1972). The question arises as to why particular males are chosen as sexual partners by female guppies. Many studies involving courtship behavior in guppies cannot answer this question directly or at all (Bastock 1967, Clark and Aronson 1951, Haskins and Haskins 1949, Farr 1976), because the female guppies, in the small aquaria involved, could not choose unambiguously to accept or reject courtship. There was no way for the female to escape if she so decided.

Investigating female choice behavior involves arranging the problem so that one is sure that it is the female which is making the courtship decision. Since females among related species do not differ among themselves in size, color, and other physical characteristics as much as males do (Selander 1965), and they tend to invest more time and energy in courtship and reproduction than males do (Trivers 1972) it follows from Fisher's (1958) theory of genetic mechanisms that males should have developed morphological characters and behaviors that closely match the females' preferences.

The mechanisms of sexual selection have received considerable theoretical treatment (Bateman 1948, Fisher 1958, Willson and Pianka

1963, Selander 1965, Verner 1965, Orians 1969, Williams 1975, Zahavi 1975, Dawkins 1976). These mechanisms relate primarily to Huxley's concepts of epigamic and intrasexual selection (Mayr 1972). Intrasexual selection involves either pre- or post-copulatory competition among members of the same sex, and can include territorial exclusion, dominance, differential ability to locate mates, mating plugs, sperm displacement, induced abortion and infanticide. Epigamic selection involves either choice made between sexual partners or differential mating success as a function of breeding time (Wilson 1975). In epigamic selection it is usually but not invariably, the female which chooses a sexual partner on the basis of showiness, sexual ability, or presence at the right time. Farr (1977) points out that instances of intrasexual selection are relatively easy to find but not those of epigamic selection. He examined the role of sexual selection in the female's choice of courtship partner and in the consequent preservation of male guppy polymorphism. He showed that intrasexual competition exists among male guppies (1976), and that females show preferences for newly introduced males that differ in coloration from males already present in a test population (1977). The latter study looked at female selection of a newly introduced rare male by noting the females' responses to male displays and by counting the broods sired by the differently colored males. He attributed the greater-than-chance success of the rare males to their selection by the females rather than to their own initiative. Yet, even in this study the females were not in complete control of the choice situation.

The concern of the present study was to investigate sexual

selection by guppies in a situation which provided the females with a means of completely controlling their courtship choices. The females were allowed to choose among males that differed in coloration or size to see if either aspect of morphology influenced their courtship preferences. Since coloration varies in male guppies, whereas size is more consistent, these two characters could both be influenced by female choice but in opposite directions. Thus females could make choices which would tend to make males more heterogeneous in one character and more homogeneous in the other. Here, the role of female choice was examined with respect to these two morphological characters.

METHOD

Subjects

The subjects of this study consisted of 120 female guppies obtained from a local supplier. The females were drab in coloration and similar in size (approximately 4-5 cm). The male guppy stimuli differed in coloration and size. The colorations were:

Fancy: They had intensely colored bodies with red and blue predominating. They had large, showy fins.

Half-Black: They were dark blue caudally to the dorsal fin and pale green elsewhere. Their fins were large and showy like those of the Fancy males.

Plain: They had whitish-gray bodies, with small fins that were blotched with small amounts of red and blue.

Two males were used from each group, a large one (approximately 3 cm long), and a small one (approximately 2.5 cm long). The same males were used for all tests.

The stimulus males were housed in part of a 76-l aquarium separated from other males by a plastic divider. The females were housed in three 76-l aquaria. At the start of the study all of the females were housed in two of these aquaria, after each female was tested she was placed in the third aquarium. The fish were brought to a uniform state of food motivation at the time of testing. They were fed in the morning, and tested in the afternoon.

Apparatus

Testing was conducted in a 76-l aquarium that was divided into

three sections by the insertion of a chamber in the center. The chamber was a tall, narrow box constructed of plywood and clear plastic which fitted tightly in the aquarium. On the two sides of the box, facing the outside aquarium sections, were fitted two wire-mesh cones pointing outwards. Figures 1 and 2 show the chamber and its dimensions. After the females were initially placed in the center of the chamber they made their choice of male by having to swim through a cone to get into the males' section. In each outside section were located two 1000-ml glass beakers submerged approximately eight cm from the cone openings, into which the males were placed. Throughout the study lighting was constant from overhead hoods and the aquaria were filtered by under gravel filters.

Procedure

Testing began with the placement of dissimilar males in opposite beakers according to the combinations listed in Table 1. After placement of the males, a female was introduced into the center chamber by means of a dipnet. When released she was oriented so that the long axis of her body was perpendicular to the long axis of the aquarium. She was then observed as she swam into one of the side chambers. After entering one of the side chambers she was removed and reintroduced in the center chamber.

Each female was tested ten times on the same pair of males, and the number of times she swam to each male's beaker was recorded. Eight females were tested for each male combination. The beakers containing the males were switched from side to side in a predetermined

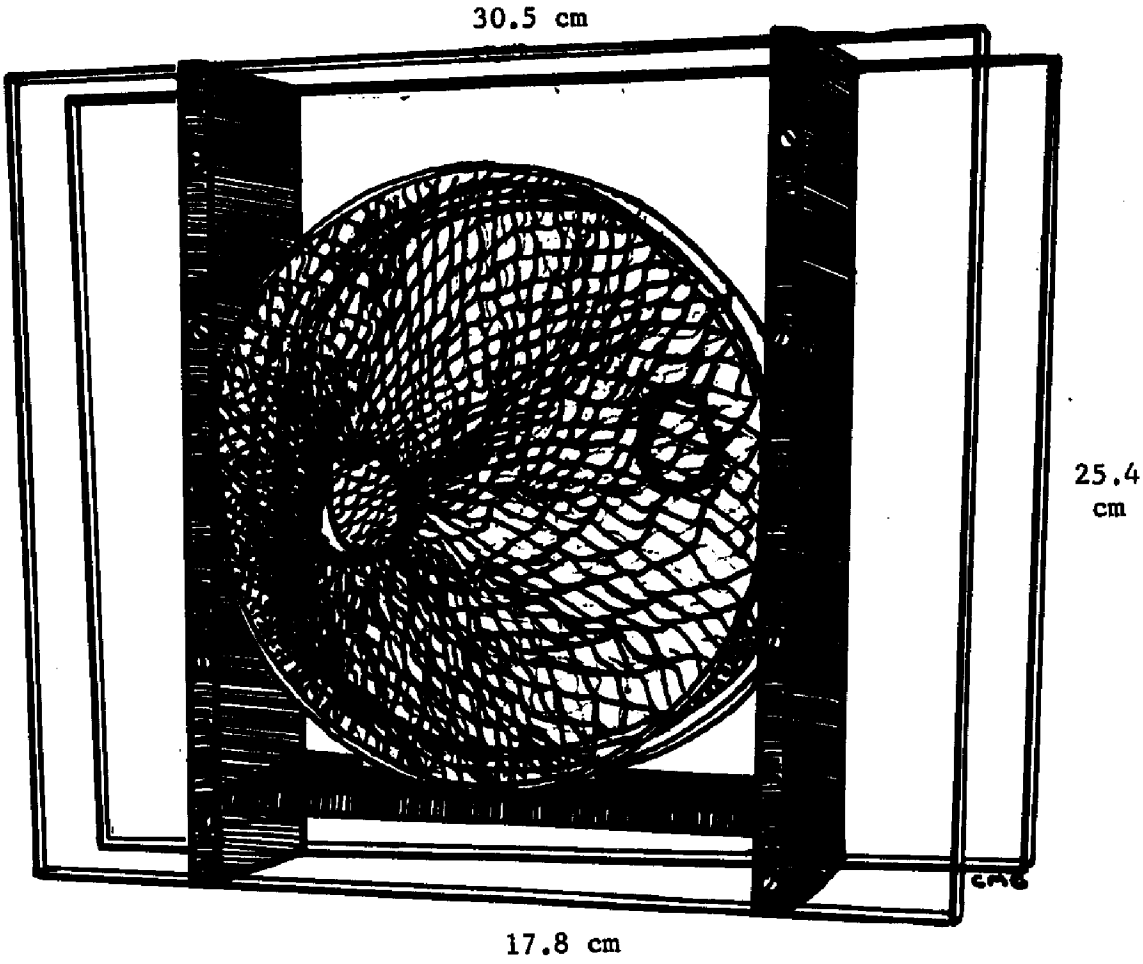

Fig. 1. Choice Apparatus (side view). (See description in text).

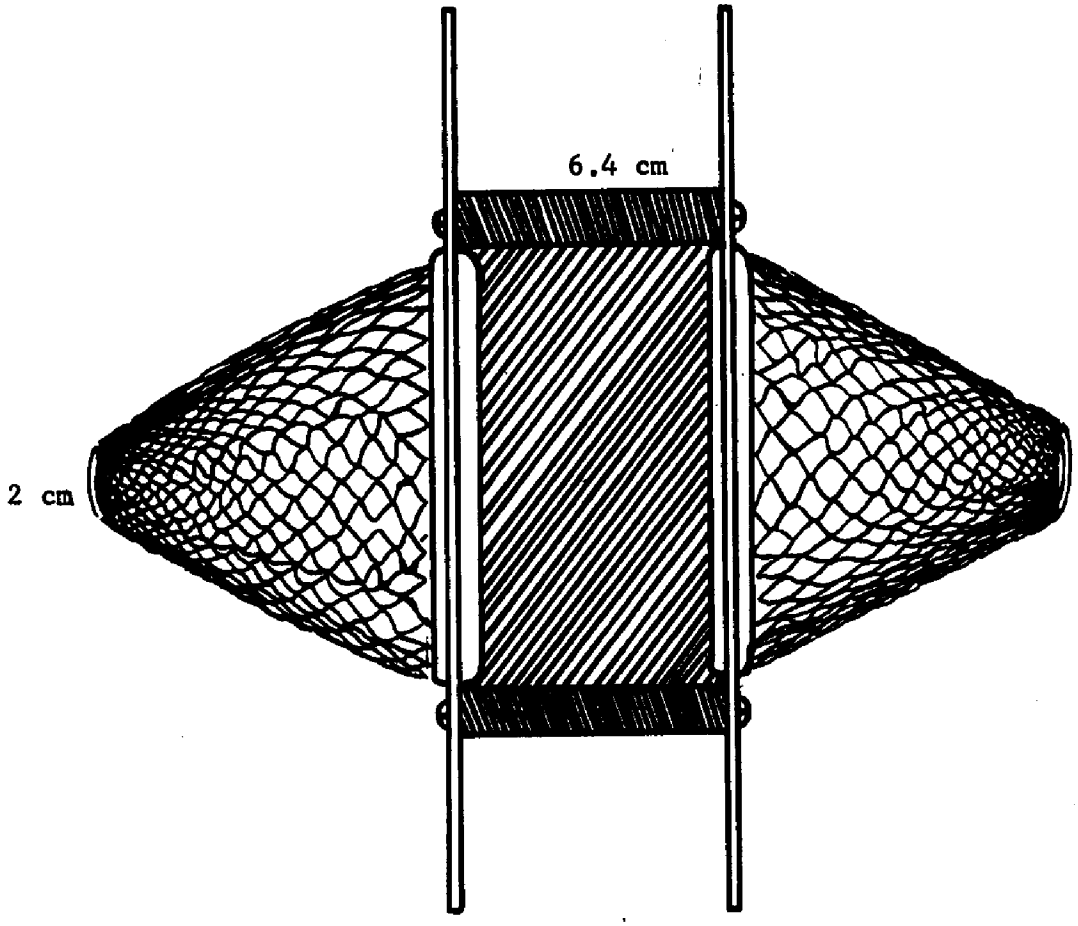

Fig. 2. Choice Apparatus (top view). (See description in text.)

Table 1

Male Combinations That Female Guppies Were Allowed to Choose From

Males	LF	SF	LHB	SHB	LP	SP
LF		x	x	x	x	x
SF			x	x	x	x
LHB				x	x	x
SHB					x	x
LP						x

counterbalanced fashion. The males were placed in beakers primarily to prevent agonistic behavior. It was hoped this would ensure that the females, by swimming to one side, were indeed being attracted to that male rather than fleeing from the other male. The beakers also served to keep the male visible to the female and in one location at all times. It was believed that these advantages outweighed the disadvantage of disrupting courtship behavior and contact. Typically, the females hesitated for some seconds in the chamber, then swam to one or both sides, before exiting.

The male combinations were tested in a random order. After all combinations were tested a ranking of the six male stimuli groups was determined, and differences among groups were tested using the chi-square test.

RESULTS

The females chose one male of a pair much more frequently than his counterpart. The most preferred males were in the Small Fancy group. They were followed in order by Large Fancy, Small Plain, Large Plain, Large Half-Black, and Small Half-Black. This ranking was determined by computing a preference ratio for each male group in the comparison pairs. The basis for the ratio was the total number of female preferences for a particular pair. Thus, for each of the fifteen experimental combinations of groups two ratios were computed, one being the reciprocal of the other. Each of the male groups generated five ratios. To rank the male groups a won-loss table was constructed from the ratios, where a ratio greater than one was counted as a win, a ratio less than one as a loss, and a ratio of one as a tie. Wins were awarded a value of 1, losses a value of -1, and ties a value of zero.

Table 2 shows the ranking, won-loss record, and points for the six male groups. It appeared from this ranking that females made their choices primarily on the basis of male coloration rather than of male size.

To test the significance of female preference, chi-square tests were performed. The significant ($p < .05$) chi-square and preference counts (Table 3) indicated that female choices were not random. Male coloration alone (Table 4) was a significant factor in selection

Table 2

Order of Preference of Male Groups Based Upon Female Choices (See Text for Explanation)

Group	Record			Points	Rank
	W	L	T		
SF	5	0	0	5	1
LF	3	1	1	2	2
SP	2	2	1	0	3
LP	1	2	1	-1	4
LHB	0	2	3	-2	5
SHB	0	4	1	-4	6

Table 3

Chi-Square Test of All Male Groups*

	LF	SF	LHB	SHB	LP	SP	Total
Observed	16	23	11	6	12	12	80
Expected	13.3	13.3	13.3	13.3	13.3	13.3	80

$x^2 = 12.25$, significant at less than .05 level.

*Table entries for all chi-squares are the number of overall preferences females showed for each group with females which showed equal preference for both males in their comparison pair excluded; there were 40 females which showed equal preference and they were evenly distributed throughout the 15 comparison pairs.

Table 4

Chi-Square Test of Coloration of Male Groups

	Fancy	Half-Black	Plain	Total
Observed	39	17	24	80
Expected	26.67	26.67	26.67	80

$x^2 = 9.47$, significant at less than .01 level.

showing that females chose males on the basis of coloration. A further chi-square (Table 5) performed because the Fancy males were chosen most often, showed that the females' preference for Fancy males was significantly greater than their preferences for either the Half-Black or Plain males. The females' choices did not differ significantly among the Half-Black and Plain males (Table 6). The chi-square distribution analysing both size and coloration simultaneously (Table 7) was not significant, nor was a chi-square comparing coloration and size with the data for the Plain males omitted. Thus, no differences were seen because of size, nor because of size within coloration. Females based their choices primarily upon male coloration.

Table 5

Chi-Square Test of Fancy Males Compared to Half-Black and Plain Males

	Fancy	Half-Black & Plain	Total
Observed	39	41	80
Expected	26.67	53.33	80

$x^2 = 8.55$, significant at less than .01 level.

Table 6

Chi-Square Test of Half-Black Males

Compared to Plain Males

	Half-Black	Plain	Total
Observed	17	24	41
Expected	21.5	21.5	41

$x^2 = 1.2$, not significant.

Table 7

Chi-Square Test Comparing Coloration and Size Among All Male Groups

	Fancy	Half-Black	Plain	Totals
Large	16	11	12	39
Small	23	6	12	41
	39	17	24	80

$x^2 = 2.69$, not significant.

DISCUSSION

Drab guppy females that were similar in size chose to be near some males over others because of their color but not because of their size. This preference satisfies the first step required determining the role of female choice in guppy courtship. The order of preference by these females was Small Fancy, Large Fancy, Small Plain, Large Plain, Large Half-Black, and Small Half-Black. The females' preference for the Fancy over the Half-Black males occurred even though the fins of the two groups are similar in size and shape, and both are intensely colored. It appears that the females selected males primarily on the basis of their color pattern and not on other characteristics. The females may have been matching the males they saw to some internally programmed specific search image (Krebs 1973), similar but not identical with the Fancy color pattern. The overall order of preference agrees with this interpretation since the second most preferred group was the Plain; what little coloration they had was similar to the Fancy males.

A condition which may affect the interpretation of these results was that the females used in this study comprised a sample more homogeneous than the population at large. Some females in the author's possession but not used in this study, like the Half-Black females were also dark blue caudal to the dorsal fin. Since these females were not used (there were only a few in the sample), it is

not possible to determine if they might have had a different search image than the females that were used. The specific search image may be a mechanism for female selection, but this study cannot determine if guppy females have one common search image or a variety of search images that depend on the genetic composition of particular females.

The fact that male guppies exist as color polymorphs in nature (Farr 1977) does little to clarify the situation. If the females, in fact, have only one common search image, then in order for polymorphy to be maintained it must be due to factors other than female choice. However, if the females' choices vary with their genetic composition such that genetically distinct females choose different males, then female choice could be the major influence in male polymorphy. The latter of these two hypotheses would be relatively easy to test using the same apparatus and controlling for female genetic strain. To test the former hypothesis would require identification of factors other than female choice such as relative proportions of male polymorphs in the population at the time of mating amd predator vulnerability of male polymorphs, which could serve to maintain them in population. Nevertheless, regardless of the mechanism involved, female guppies choose males on the basis of their color. The lack of female preference for males on the basis of size again suggests that factors other than female choice serve to maintain male size smaller and more consistent than females.

This study has allowed female guppies to choose differently

colored or sized male guppies, and has shown that the females select on the basis of color but not size. The selection of males for their physical characteristics shows that female choice may play a role in mate selection as predicted by sexual selection theory.

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VITA

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EXAMINATION AND THESIS REPORT

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Major Field: Psychology

Title of Thesis: Female preference for male coloration and size in the guppy, Poecilia reticulata

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

July 7, 1978